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WATER BALANCE DURING REAL AND SIMULATED LONG-DISTANCE MIGRATORY FLIGHT IN THE BAR-TAILED GODWIT[1]

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Abstract. We examined Bar-tailed Godwits (*Limosa lapponica*), a long-distance migratory shorebird, for evidence of dehydration toward the end of their 4,300-km migratory flight from West Africa to the Dutch Wadden Sea. Bar-tailed Godwits are ideal subjects for research on flight range constraints because they can readily be caught in migratory flight. Because godwits are capable of long nonstop travel, we hypothesized that they are physiologically adapted to minimize en route water loss, and therefore, do not experience water imbalance under standard migratory conditions. To test this hypothesis, we compared the hydration state of flying Bar-tailed Godwits at the end of a long bout of migratory flight to that of recently-landed godwits. Flying godwits were hydrated to the same degree as birds with free access to water, suggesting that godwits maintain water balance during migratory flight. To corroborate these empirical results, we ran a theoretical simulation of flight-incurred loss of water and energy in a male Bar-tailed Godwit based on the published model by Klaassen et al. (1999). When a low body drag is assumed, model output suggests that Bar-tailed Godwits flying at altitudes ranging from sea level to 3,000 m will avoid dehydration, and that flight at about 3,000 m will result in the longest possible flight range.

Key words: *Bar-tailed Godwit, dehydration,* Limosa lapponica, *migration, model simulation, stopover, water balance.*

INTRODUCTION

Bird migration requires nonstop flights of hundreds or even thousands of kilometers, especially when it involves crossing large bodies of water or inhospitable regions. During such journeys, birds are unable to feed or drink, and depend on stored energy to fuel flight and on metabolic water to maintain a physiological hydration state. Thus, the question arises as to whether depletion of water or of energy is the main factor limiting maximum range of travel during a leg of migratory flight.

Yapp (1956, 1962) first suggested that water loss is an important consideration when investigating migratory flight range. This view is in agreement with theoretical simulations of flight-incurred water and energy loss in a small migrating passerine, whose calculated flight range is constrained by water imbalance (Carmi et al. 1992, Klaassen 1995, Klaassen et al. 1999). Field studies that claim dehydration in migrating passerines landing on a ship in the Atlantic Ocean (Searle 1956), and in various passerine species caught soon after crossing the Sahara Desert (Fogden 1972) or the Gulf of Mexico (Leberg et al. 1996), support the hypothesis that water supply may limit maximum distance traveled. However, methods utilized by some of these field studies are questionable: in one case

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the body water of birds was not quantitatively measured (Searle 1956); in another, the effect of body composition on water content was not taken into account (Leberg et al. 1996). In addition, these studies only investigated birds that had landed to rest or refuel, allowing the possibility that some of these migrants had discontinued flight because of abnormal exhaustion. Therefore, even if data had been analyzed correctly, the possible inclusion of a disproportionate number of dehydrated birds renders results from these studies inconclusive.

In contrast, other investigations suggest that dehydration is not a serious limitation to migratory flight range. An earlier study of landed passerines that had crossed the Gulf of Mexico found no evidence of dehydration (Child 1969). Dying Willow Warblers *Phylloscopus trochilus* and other small passerines in a stopover site in the Sahara also displayed normal water balance, even though they had depleted fat stores (Biebach 1990). Although data from these studies support an energy-limiting hypothesis, they are inconclusive in that the examination of landed migrants allows the possibility that subjects had rehydrated before sampling.

Previous studies were unable to definitively assess whether water imbalance is a factor in the determination of migratory flight range because only landed, rather than in-flight, migrants were examined. In-flight migrants are better suited for the investigation of flight range constraints because their physiology is more representative of a migrating individual's state. To date, only one site—the alpine pass Col de Bretolet, Switzerland (Jenni-Eiermann and Jenni 1991, 1992, Gwinner et al. 1992)—has been utilized for field research on migratory flight. Unfortunately, research at this site has not included measurements of bird hydration state.

Bar-tailed Godwits *Limosa lapponica* are long-distance migrant shorebirds that can readily be caught in migratory flight, and are therefore excellent subjects for the investigation of hydration state during migration. Bar-tailed Godwits initiate spring migration in West Africa and fly nonstop to their main refueling site in the Wadden Sea of The Netherlands, Germany, and Denmark (Piersma and Jukema 1990). During this 4,300-km migratory journey, metabolic water is the only water source, while water losses result from both excretion and evaporative cooling. Because water imbalance results in decreased oxygen provisioning to tissues (Horowitz and Samueloff 1986, 1987) and a high internal heat load (Feig 1981, Horowitz 1984), flying migrants that experience dehydration need to land to rehydrate. Changes in flight altitude during landing and takeoff are energetically expensive and may cause further migratory delay if depleted energy stores need to be restored. We therefore hypothesized that for timely and successful migration, Bar-tailed Godwits have adapted their behavior and physiology to minimize water loss during travel. We consequently predicted that godwits would not be dehydrated at the conclusion of a long-distance bout of migratory flight. To test this prediction, we collected empirical data on the hydration state of migrating godwits flying into their Wadden Sea stopover site after a 4,300-km nonstop journey from West Africa. We also ran a theoretical simulation of flight-incurred loss of water and energy in a male godwit traveling along this route.

METHODS

STUDY ANIMALS

The Bar-tailed Godwits sampled in this study winter in Mauritania and Guinea-Bissau, West Africa. They breed on the Taimyr Peninsula, Russia (Cramp and Simmons 1983, Piersma and Jukema 1990) and have recently been assigned the subspecies status *L. l. taymyrensis* (Engelmoer and Roselaar 1998). These godwits initiate spring migration from West Africa in late April (Piersma et al. 1990a), and arrive on their main refueling site, the Wadden Sea of The Netherlands, Germany, and Denmark (Glutz et al. 1977, Piersma and Jukema 1990), three days later. Bar-tailed Godwits spend about 4 weeks feeding in the Wadden Sea area before departing on a nonstop flight to their northern breeding grounds in early June (Boere and Smit 1981, Piersma and Jukema 1990).

We sampled 19 Bar-tailed Godwits caught during spring migratory flight at a site only 60 km short of the Wadden Sea stopover area, in the dunes of Castricum, The Netherlands (53°32′N, 04°37′E) (Fig. 1). Bar-tailed Godwits captured in Castricum are examples of birds at the end of a long bout of migratory flight and are henceforth referred to as arriving godwits. Although godwits do not normally land in Castricum, spring migratory flocks regularly fly overhead from late April to early May. Passing

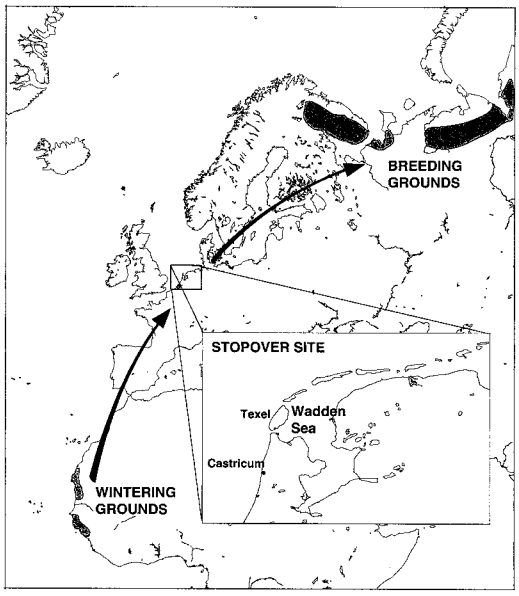

FIGURE 1. Spring migratory route and stopover site of the Bar-tailed Godwit. Godwits were caught at two sites in The Netherlands: flying godwits arriving into the stopover area were intercepted in the dunes near Castricum, and refueling godwits were captured on the island of Texel.

flocks were successfully lured from the sky by exposing them to call playbacks and decoys, and were captured during daylight hours with clap nets immediately upon landing from 1–6 May 1998.

To determine whether Bar-tailed Godwits suffer from dehydration during long-distance migratory flight, we compared the water content of arriving godwits to that of godwits that had recently landed in the Wadden Sea, where they had the opportunity to achieve a physiological hydration state. The body composition of these recently-landed godwits should be similar to that of arriving godwits. A meaningful comparison of hydration states requires that compared individuals have similar body composition: although total body water (TBW) varies in a constant proportion to lean body mass, relative TBW decreases as individuals gain fat mass because adipose tissue holds little water (Child 1969, Ellis and Jehl 1991).

We captured landed godwits during daytime on the island of Texel (53°03′N, 04°48′E) (Fig. 1), a Wadden Sea stopover site, with a large pull-net, the ''wilsternet'' (Koopman and Hulscher 1979), during the period of 13–21 May 1998. Because godwits steadily increase in body mass after arrival to the Wadden Sea (Piersma and Jukema 1990), we subjectively selected 25 light, presumably recently-landed, godwits (referred to as early-refueling godwits) from the total catch of landed birds. Because average body mass of these early-refueling godwits was still relatively low—262 g and 301 g for males and females, respectively; compared to 390 g and 470 g for fully refueled godwits (Piersma and Jukema 1990)—these birds had probably been in the Wadden Sea area for less than two weeks. During this time they had ample opportunity to drink and rehydrate at intertidal mudflats and at the many nearby freshwater sites.

SAMPLING

Captured Bar-tailed Godwits were banded, weighed, measured, and sexed (Piersma and Jukema 1990). TBW was determined with the deuterium isotope (D_2O) dilution technique (Speakman 1997). We injected each bird subcutaneously with 0.3 g D_2O (99.8% deuterium). The exact dose each bird received was later verified by weighing the refilled syringe to the nearest mg. After injection, birds were kept in cloth bags during a 1-hr equilibration period (Speakman 1997). We then punctured the brachial vein with a sterile needle and collected a 15-μL equilibrated blood sample into each of six micro-capillary tubes. To determine background levels of deuterium, we collected additional blood samples from three non-D_2O injected birds on Texel. Samples were prepared and measured as described in Visser and Schekkerman (1999).

TBW for each bird was calculated using the average ^2H enrichment of the three background samples (C_b, atom percent), the quantity of the dose (Q_d, moles), the ^2H enrichment of the dose (99.8%), and the ^2H enrichment of the equilibrium blood sample as assessed from triplicate isotope analysis (C_{eq}, atom percent) as follows:

$$\text{TBW (g)} = [Q_d \cdot 18.02 \cdot (99.8 - C_{eq})/(C_{eq} - C_b)] \div 1.04$$

The value 18.02 is used to convert units from moles to grams, and the factor 1.04 is employed to correct for minor over-estimations of body water with ^2H (Speakman 1997). We divided TBW by body mass for each bird to calculate percent body water (%BW)—a measure of water

content that eliminates effects of size differences in subjects with similar body composition.

STATISTICAL ANALYSES

We used analysis of covariance (ANCOVA) to compare %BW between arriving and early-refueling godwits. Migratory status (arriving or early-refueling) was included as a factor. After verifying the homogeneity of slopes between body mass and migratory status, we included body mass as a covariate. ANCOVA models were constructed separately for each sex because Piersma and Jukema (1990) found that at any given body mass, body composition differs between sexes. We therefore present the average %BW of male and female godwits without considering statistical differences. Data satisfied both the normality and constant variance tests. Values listed in results are means ± SD. Differences in body mass between arriving and early-refueling Bar-tailed Godwits were examined separately for each sex with a Mann-Whitney *U*-test.

We excluded one outlier from data analysis—a light arriving female with a %BW of 45%. Because this godwit was at the end of a long-distance flight, most of its fat stores were depleted (Piersma and Jukema 1990). Carcass analysis has revealed that the water content of fat-free mass in Bar-tailed Godwits varies from 65 to 69% (Piersma and van Brederode 1990). Because the value of 45% is well outside this observed range, the outlier is not likely to be a real example of a dehydrated bird. Instead, because the outlier was the first bird measured, its abnormally low water content reading is more likely due to our initial inexperience in the D_2O technique.

MODEL SIMULATION

We used software recently developed by Klaassen et al. (1999), which builds on the model of Carmi et al. (1992), to simulate water and energy loss during the migratory flight of a male Bar-tailed Godwit from Banc d'Arguin, West Africa to the Dutch Wadden Sea. To investigate how travel at different altitudes may affect flight range constraints, we ran simulations at sea level, 1,500, 3,000, and 5,500 m altitude, assigning head-winds for the lowest two altitudes and tail-winds for the highest two altitudes as derived from atmospheric data by Piersma and van de Sant (1992). We assumed an average decrease in temperature of 6.5°C 1,000-m^{-1} increase in altitude. The specific parameter values used in the Bar-tailed Godwit simulation that were altered from the original settings in Klaassen et al. (1999) are as follows: fat fraction—0.26, body mass—0.35 kg, wingspan—0.66 m, initial %BW—45%, bird type—non-passerine. Parameter values for Bar-tailed Godwits were obtained from Piersma and Jukema (1990), Lindström and Piersma (1993), and the present study. Because body drag produced by a flying godwit has not been determined, we ran multiple simulations with the body drag coefficient set at 0.05, 0.06, 0.07, and 0.08—a range of values considered likely for streamlined birds (Pennycuick et al. 1996), such as the Bar-tailed Godwit.

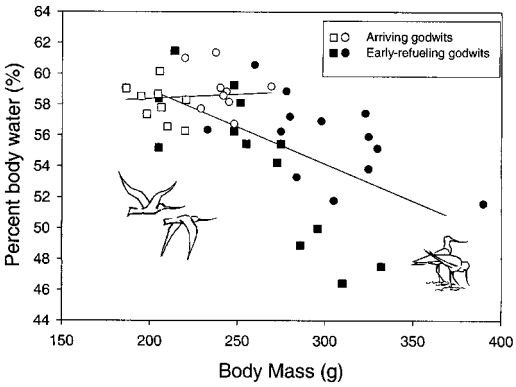

FIGURE 2. Percent body water (%BW) as a function of body mass in arriving and early-refueling Bar-tailed Godwits sampled in spring of 1998, The Netherlands. Drawn lines represent linear regressions for each capture site. Males are designated by squares, females by circles.

RESULTS

Percent body water (%BW) of arriving and early-refueling Bar-tailed Godwits was 58.1 ± 1.2% and 54.4 ± 4.8%, respectively for males, and 59.0 ± 1.5% and 55.8 ± 2.6% for females. There was no difference in %BW between arriving and early-refueling godwits (ANCOVA: $F_{2,19} = 27.9$, $P = 0.17$ for males and $F_{2,19} = 11.3$, $P = 0.44$ for females) (Fig. 2). %BW decreases with increasing body mass in both sexes (ANCOVA: $F_{2,19} = 27.9$, $P < 0.001$ for males and $F_{2,19} = 11.3$, $P < 0.05$ for females) (Fig. 2). Even though we attempted to sample only low-mass refueling birds to ensure similarities in body composition between the two study groups, the body mass between arriving and ear-

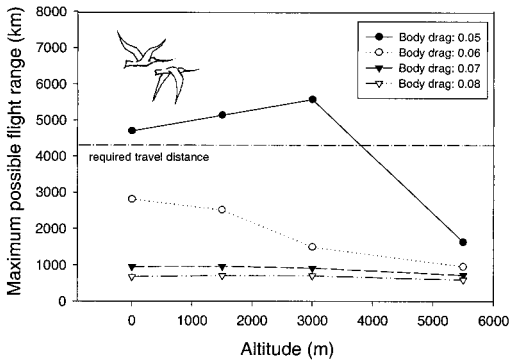

FIGURE 3. Model output for the simulated migratory flight of a male Bar-tailed Godwit from Banc d'Arguin, West Africa to the Dutch Wadden Sea. Simulations were run at different altitudes and at different body-drag coefficients. The migratory distance that must be completed is 4,300 km, and is indicated by the horizontal dashed line.

ly-refueling godwits was nevertheless significantly different ($U = 57$, $P < 0.05$ for males and $U = 53$, $P < 0.001$ for females). We therefore recalculated %BW for early-refueling godwits from only those birds whose mass overlapped with that of arriving godwits. The %BW of arriving and early-refueling godwits that were of similar body mass was 58.0 ± 1.4% and 58.4 ± 3.1%, respectively for males, and 58.8 ± 1.4% and 58.4 ± 3.0% for females. When all godwits were considered, male and female %BW was 55.9 ± 4.1% and 57.1 ± 2.7%, respectively.

Output of model simulations predict that Bar-tailed Godwits are not able to complete the required 4,300-km migratory flight if body drag is greater than 0.05 (Fig. 3). Water imbalance is the cause for the discontinuation of flight in all cases where the calculated flight range of Bar-tailed Godwits falls short of 4,300 km. If water balance is maintained, godwits are able to complete flights of 4,300 km or more, which are then terminated as a result of energy shortage. When it is assumed that Bar-tailed Godwits have a body drag of 0.05, maximum flight range steadily increases with altitude up to 3,000 m, but drops at an altitude of 5,500 m (Fig. 3).

DISCUSSION

Our hypothesis that water shortage does not normally limit the migratory flight range of Bar-tailed Godwits is supported by the collected empirical data: Bar-tailed Godwits captured in flight, at the end of their 3-day migratory journey from West Africa to the Dutch Wadden Sea, showed no indication that they were dehydrated. Decreased body water would be expected in at least some late-flight birds if water imbalance were the main cause for the discontinuation of migratory flight. However, a comparison of the hydration state of arriving godwits to that of early-refueling godwits which have the opportunity to drink near feeding areas revealed no differences.

Water loss during flight results from excretion and evaporative cooling, where evaporative cooling includes both respiratory and cutaneous evaporation. Migrating Bar-tailed Godwits may be able to maintain water balance by minimizing these processes of water loss through behavioral or physiological mechanisms. Most significantly, migrating godwits may alter behavior by flying at higher altitudes where ambient temperatures are sufficiently low to dissipate heat by convection, and thus minimize water lost through evaporative cooling (Torre-Bueno 1978, Biesel and Nachtigall 1987, Nachtigall 1995). Wind tunnel tests of pigeons (*Columba livia*) wearing respiratory masks show that birds are able to maintain water balance only when ambient temperature is less than 10°C (Biesel and Nachtigall 1987)—a limit that may be higher during free-flight, when weight and thus energy expenditure is lower. On the other hand, godwits should not fly above certain critical altitudes: although lower ambient temperatures at higher altitudes decrease the need for evaporative cooling, lower partial oxygen pressures increase respiration frequency (cf. Fig. 3), and thus water loss through exhaled water vapor.

In addition to behavioral changes, modifications of physiological function may help to maintain water balance in migrating Bar-tailed Godwits. Godwits may maximize their ability to conserve respiratory water vapor via countercurrent heat exchange mechanisms, as has been observed in several bird species (Schmidt-Nielsen et al. 1970, Murrish 1973). Godwits may also increase the efficiency of oxygen-extraction to decrease respiration frequency and the accompanying loss of water vapor in exhaled air (Carmi et al. 1992). Piersma et al. (1996) showed that Bar-tailed Godwits elevate red blood cell number prior to departure from the Dutch Wadden Sea in spring and thereby increase their oxygen extraction ability prior to migratory flight.

Additionally, godwits possibly minimize excretory water losses—a phenomenon that has been demonstrated in pigeons that decrease urinary output during flight (Giladi et al. 1997).

In contrast to the multiple mechanisms for water loss during flight, free water can only be gained from the catabolism of body tissues. To maintain water balance, migrants may therefore increase protein catabolism, which releases six times more water per unit energy produced (i.e., per distance flown) than fat breakdown (Jenni and Jenni-Eiermann 1998, 1999). Evidence that Bar-tailed Godwits lose a significant amount of muscle mass during migratory flight (Piersma and Jukema 1990) suggests that these migrants catabolize protein, and may therefore use the mechanism of increased protein breakdown to balance water losses. Clearly, opportunities for water conservation during migration exist. The strategies actually employed by Bar-tailed Godwits remain to be determined.

Even though Bar-tailed Godwits increase muscle mass during refueling, much of the mass gain also consists of lipid stores (Piersma and Jukema 1990). Because lipids hold less water than fat-free tissues, body mass in refueling godwits increases more quickly than total body water. Therefore, the drop in %BW with mass gain on the Wadden Sea stopover site (Fig. 2) can be explained as an effect of an increasing fat fraction (Ellis and Jehl 1991). The slightly lower %BW in male versus female Bar-tailed Godwits—a pattern that is especially pronounced in heavier birds (cf. Fig. 2)—also may be an effect of differences in relative amounts of fat-free tissue and lipid stores. For any given body mass, males deposit relatively more lipid stores than females (Piersma and Jukema 1990, Lindström and Piersma 1993)—most likely a result of the relatively smaller structural size of male godwits.

Empirical data show no indication that Bar-tailed Godwits are dehydrated at the conclusion of migratory flight, and therefore suggest that water loss is not the immediate constraint to migratory flight range in this species. Rather, the depleted fat stores of godwits arriving into the Wadden Sea stopover site (Piersma and Jukema 1990) suggest that under standard migratory conditions the flight range of Bar-tailed Godwits is limited by energy stores. The late-flight godwits evading capture in Castricum frequently started to feed, but were never observed to drink, thus supporting an energy-limiting hypothesis (pers. observ.). However, the maintenance of water balance may contribute to the depletion of energy stores. Godwits choosing to fly at higher and thus cooler altitudes to minimize evaporative water losses may expend more energy to power flight because gains in flight altitude are energetically costly. Thus, even though we suggest that energy is the primary constraint to the flight range of Bar-tailed Godwits, it is nevertheless possible that the need to maintain water balance quickens the depletion of energy stores, and therefore the discontinuation of flight.

Output of theoretical simulations predict that Bar-tailed Godwits can complete the 4,300-km nonstop flight from West Africa to the Wadden Sea only if water losses are minimized; in all cases where calculated flight range falls short of 4,300 km, the limiting factor is water supply. Thus, model results suggest that water balance is more critical than energy supply for long-distance travel. This interpretation of model results is not contradictory to the collected empirical data—model simulations reveal a window of opportunity for Bar-tailed Godwits to maintain water balance during their 4,300-km flight. The specific conditions under which this may occur are discussed below.

In our model, Bar-tailed Godwits with a body drag coefficient greater than 0.05 are unable to complete the required travel distance in one bout of flight when tailwind strength as derived from atmospheric data is assumed. We therefore confine subsequent discussion to simulations that assume a body drag coefficient of 0.05, i.e., to simulations which predict a successful completion of the required 4,300-km flight under typical wind conditions.

Simulations that assume a body drag coefficient of 0.05 suggest that travel at different altitudes affects maximum flight range differently. First, the simulations predict that as Bar-tailed Godwits increase their height of travel from sea level, flight range increases to maximum length at 3,000-m altitude (Fig. 3). Simulated flights at altitudes of up to 3,000 m are constrained not by water shortage, but by a dwindling energy supply. Model results are therefore compatible with empirical data because both suggest that in successfully migrating godwits, energy depletion is the cause for the discontinuation of flight. Travel at 3,000-m altitude extends migratory

range as a consequence of increasingly favorable wind conditions and lower air density, both of which decrease energy use during flight.

Second, the model predicts that Bar-tailed Godwits flying at higher altitudes, such as at 5,500 m above sea level, will be unable to complete the long-distance flight to the Wadden Sea nonstop. Flight at 5,500 m is prematurely terminated as a result of water imbalance. As mentioned above, flight at very high altitudes increases ventilation rate and thus respiratory water loss due to low partial oxygen pressure. Model output thus predicts that godwits should fly at altitudes of about 3,000 m to achieve maximum flight range. Field studies support model predictions—migrating shorebirds departing from West Africa were observed to fly at altitudes of 1,500 m and higher (Piersma et al. 1990b), and migrating Red Knots *Calidris canutus*, a species closely related to Bar-tailed Godwits, were recorded at altitudes of up to 3,000 m over the Gulf of Finland (Dick et al. 1987).

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